THE MAXILLARY AND MANDIBULAR BREATHING VALVES OF TELEOST FISHES.

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WHILE watching the living fishes in the aquaria of the United States Fish Commission at Woods Holl, Mass., the writer noticed that the jaws were scarcely moved in breathing, the mouth being kept open all the time, except when used for biting or for yawning, or other acts than breathing. Further, when the fish was facing the observer and when the light was favorable a pair of large and well-developed membranous valves were seen inside the mouth, opening and shutting with a perfect automatic motion as the fish breathed.

One of these valves, which were both situated just inside of the teeth, depended from the roof of the oral cavity, while the other arose to meet it from the floor of the oral cavity just in front of the tongue. They were crescentic in shape, widest directly in front, and tapering down laterally to a point just behind the angle of the mouth. Their lines of attachment to the surfaces of the oral cavity were concentric with the teeth. In texture they were semi-transparent and extremely flexible and strong.

A few minutes' observation was sufficient to demonstrate that these structures were valves of great importance in breathing; and an examination was made of the literature on the subject.

No mention of such valves appears in the standard works on ichthyology and comparative anatomy, with the exception of Owen,[1] who says: "The folds of membrane behind the upper and lower jaws, of which 'internal lips' the swordfish and dory afford good examples, seem intended to prevent the reflux

[1] Owen, Anatomy of Vertebrates, vol. i, p. 413. London. 1866.

of the respiratory stream rather than the escape of food from the mouth."

Gunther[1] makes no mention of the organs in question, and states that "the water used by fishes for respiration is received by the mouth and by an action similar to that of swallowing is driven to the gills and expelled by the gill openings." I have found several differences between the acts of swallowing and of breathing in the teleost fishes.

Wiedersheim[2] states that "fishes breathe by taking in water through the mouth and, by the contraction of the latter, forcing it out again through the gill slits."

The use of the word "through" in the above quotation leads me to infer that the mouth opening is meant, and not the oral cavity.

A. B. Macallum[3] has mentioned these structures in his article on the "Anatomy of Amiurus," where he says: "Behind the pads of teeth and running concentrically with them are folds, one above and one below, arising from a relaxation of the lining membrane; that behind the maxillae is largest, but both may be absent. In one specimen of *Amiurus nigricans* the fold reached downward and backward into the cavity of the mouth fully one-half inch." No mention of the function of these folds of membrane is made.

These valves have been observed in operation by the writer in over fifty species of fresh-water and marine fishes, and no teleost has been found which does not possess them. Since no accurate description of them and of their function has become part of our recent manuals or text-books, and since, on the other hand, for want of such knowledge it has been impossible to clearly describe the act of breathing in fishes, I take this opportunity of calling attention to these valves and of demonstrating their value as organs of breathing.

These valves will first be described as they appear in the common sunfish, *Eupomotis gibbosus* (Linn.). (See Fig. 1.)

[1] Gunther, Introduction to Study of Fishes, p. 136. Edinburgh. 1880.

[2] Wiedersheim (translated by W. N. Parker), Comparative Anatomy of Vertebrates, p. 278. London. 1896.

[3] *Proc. of Canadian Inst.*, N.S., vol. ii, No. 3, p. 387. Toronto.

In this fish they are highly developed and efficient. The upper valve is a sheet of membrane hung from the roof of the oral cavity and covered by a continuation of its mucous membrane. Its line of attachment is slightly bow-shaped, and lies directly behind the teeth and parallel with them.

The valve is broad with a straight lower edge, in the middle of which is a thickened tooth-like projection. This projection

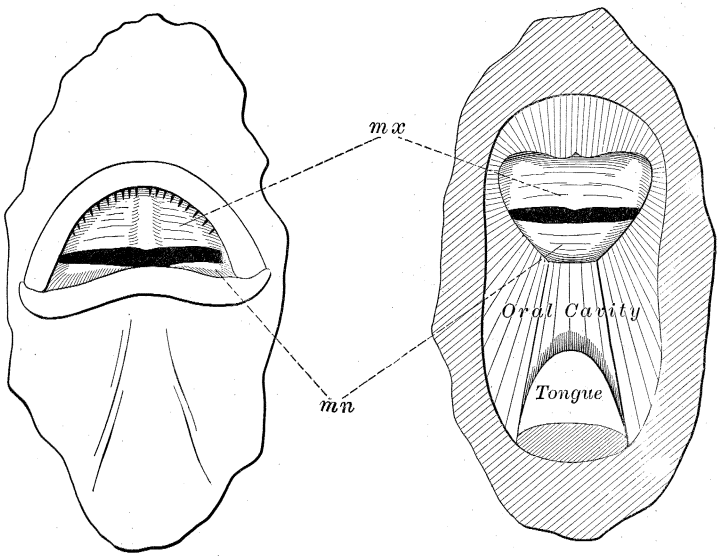

FIG. 1. — Maxillary and mandibular breathing valves of sunfish, *Eupomotis gibbosus* (Linn.). Seen from in front (*A*), and from behind (*B*). *mx.*, maxillary breathing valve; *mn.*, mandibular breathing valve.

is the lower end of a vertical median thickening of the valve. The lower valve is two-thirds as broad as the upper, and in other respects is similar to it. The median thickening is perhaps not so marked, and the valve tapers more at each lateral extremity. Sections show that each valve is a membrane of elastic connective tissue covered with a mucosa. The mucosa possesses a well-developed layer of smooth muscle, while a layer of the same kind of muscle extends from anterior surface to posterior surface at the base or line of attachment of the valve. In death the valves are found lying close to the surface of the

oral cavity with their free edges pointing backward, and if the specimen has been hardened they are more easily seen. (See Fig. 2.)

In fresh dead specimens they are very hard to detect because of their flexible texture and tapering edges, which allow them

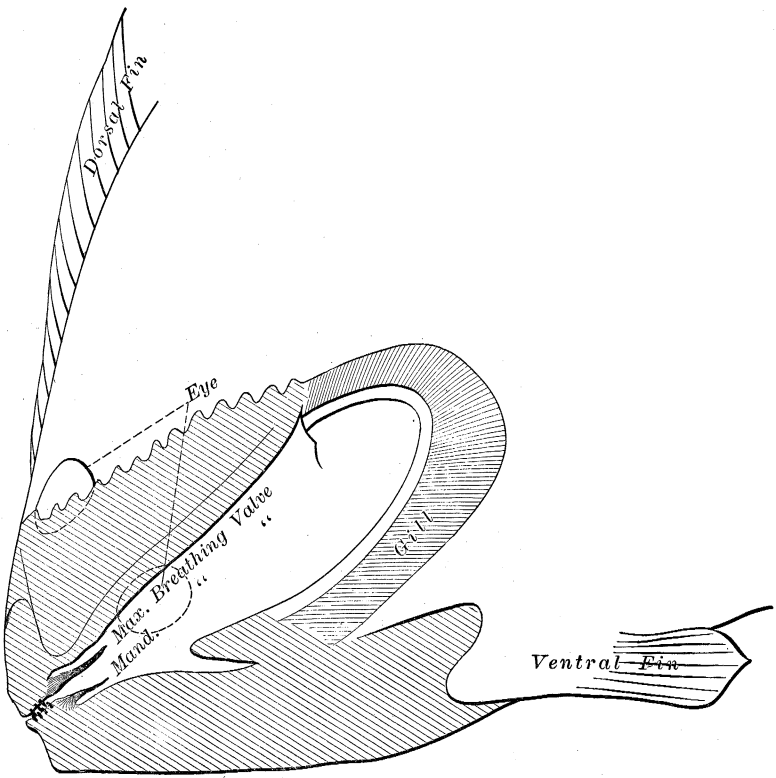

FIG. 2. — Head of flounder, *Paralichthys dentatus* (Linn.), seen from left (upper) side. The shaded area represents a vertical median section of the mouth and oral cavity to show the position of the breathing valves in an alcohol hardened specimen.

to adhere so closely to the mucous membrane of the oral cavity.

Both valves are placed with their edges pointing downward and backward at an angle of less than 45° to the axis of the body. This angle is increased to about 80° when the valves are struck by the regurgitating stream of water at the beginning of expiration.

A number of young black bass, *Micropterus salmoides* (Lac.), were carefully kept in aquaria with running water, and when they had become perfectly tame, in some weeks' time, observations were made on the rate and manner of breathing, with particular reference to the valves under consideration.

Each breath requires two acts: one of inspiration and one of expiration. During inspiration the oral cavity is enlarged by moving the opercular frames outward, thus requiring an incoming stream of water to fill the extra space produced. This stream enters the oral cavity at the mouth, which at the beginning of inspiration is open about one-fourth of its normal maximum extent. During inspiration the mouth is opened about ten per cent more, this motion being due only to the connection of the jaws with the opercular frames.

The mandibular and maxillary breathing valves are flattened back against the top and bottom of the oral cavity by the entrance of this stream of water. Meanwhile water would enter at the gill openings, which are widening, was it not for the branchiostegal membranes which, although they are attached to the opercular frames, move independently of and contrary to them, closing the entrance automatically by the action of the water that tries to enter. (See Fig. 3.)

The opposite act of expiration now takes place, the opercular frames moving inward to reduce the space in the oral cavity. The water tries to leave at the mouth, but catching on the edges of the breathing valves and then striking their posterior surfaces it forces them up into such a position that their edges meet and all further progress is stopped. The water then leaves at the gill openings.

During expiration the mouth is slightly shut, both this and its opening during inspiration being unavoidably due to the attachment of the jaws to the opercular frames, and not to an effort to retain or let out the water.

One fish of this lot was six and one-half inches long. When at rest and free from recent excitement, the number of breaths each minute was forty, with the temperature of the water at 10¾° Centigrade.

This rate was very constant, and the half-yawns which the

fish occasionally gave did not disturb the rate because they also occurred at regular intervals. The fish was taken out in a scoop-net and held gently in a wet cloth while both valves were

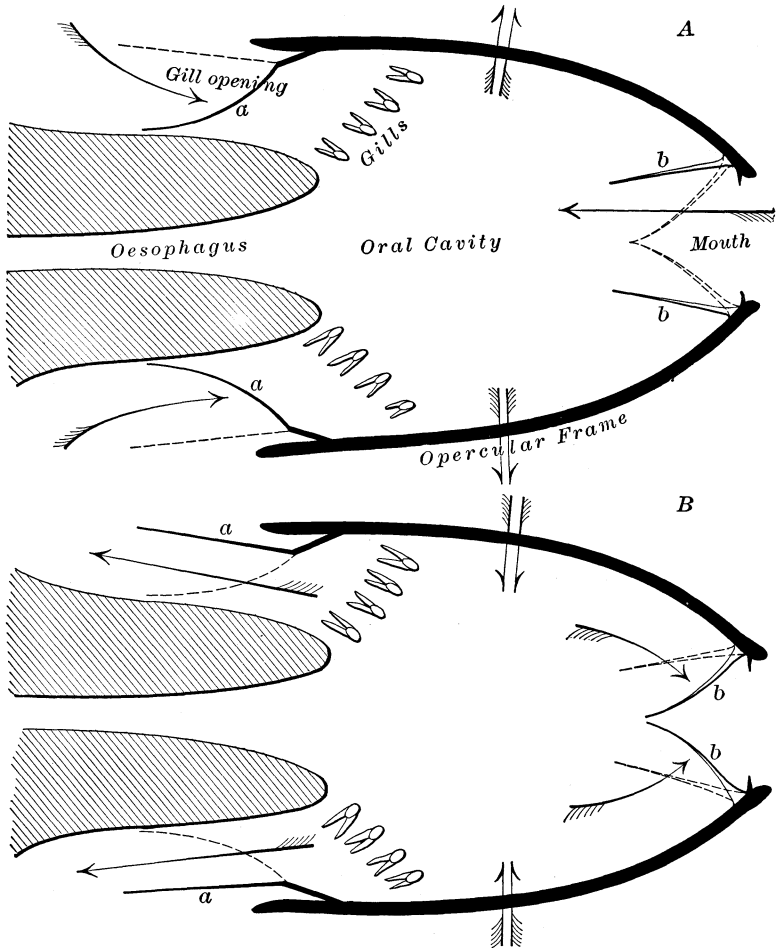

FIG. 3. — Diagrammatic representation of the pump-like structure of the teleost oral cavity. The anterior portion of each figure is represented in longitudinal vertical section, the posterior portion in longitudinal horizontal section. *A*, inspiration; *B*, expiration. Arrows represent water pressures; double arrows represent motions of opercular frames. *a*, branchiostegal valves; *b*, maxillary and mandibular breathing valves.

cut in their median line from edge to line of attachment, thus practically destroying their usefulness as valves. When returned to the water the fish darted about, but soon settled down and

in twenty minutes had apparently recovered from the effects. The rate was now fifty-nine per minute, and the manner of breathing had entirely changed. The enlargement of the oral cavity was fully a third greater than before (on a rough estimate), and at or before the beginning of expiration the mouth was tightly closed with an effort in order, apparently, to prevent the regurgitation of water. In four days this fish was breathing normally again and the valves were apparently repaired, the scar being visible on the edge as a notch, with a white line running from this notch to the line of attachment of the valve.

SUMMARY.

In the light of the above observations and experiments the act of breathing in the teleost fishes may be described as follows:

The respiratory stream enters the oral cavity by the mouth and leaves by the two gill openings, coming in contact with the respiratory surfaces of the gills just before it passes out. It is urged on its course by the pump-like construction and action of the oral cavity and its two sets of valves, an anterior set, which are those under consideration, and a posterior set, the branchiostegal valves.

In inspiration the stream enters at the mouth, in response to a dilation of the oral cavity produced by the outward lateral movement of the opercular frames.

At the same time water is prevented from entering at the gill openings by the branchiostegal valves which, although they are attached to the opercular frames, move independently of and contrary to them; so that, while this outward movement of the frames extends the gill openings, the branchiostegal valves close them automatically by the action of the water which tries to enter.

In expiration the water is forced out of the gill openings by a corresponding contraction of the oral cavity. At the same time the water is prevented from regurgitating through the mouth, not by the contraction of the latter, but by the automatic operation of the maxillary and mandibular breathing valves

which move as accurately and efficiently as any of the heart's valves. Caught on their posterior edges by the first movement of regurgitation, they snap together and completely prevent any water from leaving the oral cavity by the mouth which, meanwhile, is left partly open, almost as much open as during inspiration.

That these valves are of value as breathing organs is evident upon casual observation; that they are of much importance is shown by the compensatory action brought about by injury; that they are not of immediate vital importance is proved by the fish's ability to get along without their services until they are repaired.